

## ON THE "HABITUS" AND "HERITAGE" OF CÆNOLESTES

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The more closely one studies Dr. W. H. Osgood's excellent monograph on *Cænolestes*<sup>1</sup> the more one must be grateful to him for the quality and range of his plates, for the thoroughness of his comparisons (within the limits of available material) and for his eminently fair and impartial presentation and analysis of the difficult subject of the precise relationships of that animal to other marsupials. Doctor Osgood's monograph has already been reviewed in a recent number of this journal<sup>2</sup> and I have no wish to offer detailed criticisms or to challenge the author's main conclusions. But a careful study of this work and of Lönnberg's recent brief paper<sup>3</sup> has resulted in the following preliminary and partial analysis, in which an attempt is made, first, to bring out the correlation of habit and structure, and secondly, to make a beginning towards separating those features which have been acquired during the present life habits (habitus) from those which have been inherited from previous life habits (heritage).<sup>4</sup> Unless otherwise noted the statements of anatomical fact are to be credited to Osgood.

## I. LIFE HABITS AND ECOLOGY

1. *Geographic Distribution.* Present: Andes of Venezuela, Colombia, Ecuador, Peru. Past: *Cænolestes* is a survivor of the Santa Cruz Miocene Epanorthidæ (Palæothentidæ) of Patagonia.

2. *Life Zone.* Cool, dense forests at high altitude, 6 to 12 thousand feet, near timber line. Also in grassy openings of mountain valleys. *Cænolestes* lives in dense growth, beneath the canopy of the tree tops and still further shaded by masses of low vegetation. Osgood infers that it is crepuscular or nocturnal in habits. Found in runways among the thick grass in swampy ground, about on a level with the water line of the swamp. Lönnberg (1921) says it is arboreal in habits, but this seems doubtful.

<sup>1</sup> A Monographic Study of the American Marsupial, *Cænolestes*. Field Mus. Nat. Hist., Zoöl. Ser., vol. 14, no. 1, pp. 1-162, May, 1921.

<sup>2</sup> Journ. Mammal., vol. 2, no. 4, pp. 241, Nov., 1921.

<sup>3</sup> A Second Contribution to the Mammalogy of Ecuador, with some remarks on *Cænolestes*. Arkiv. f. Zoöl., Bd. 14, no. 4, pp. 1-104, 1921.

<sup>4</sup> Gregory, 1913. Locomotive Adaptations in Fishes, Illustrating "Habitus" and "Heritage." Ann. N. Y. Acad. Sci., pp. 267-268; Osborn, 1917. Heritage and Habitus, Science, N. S., vol. xlv, no. 1174, pp. 560-561.

3. *Food Habits.* Examination of three stomach contents reveals remains of weevils, caterpillars, lepidopterous pupa, adult lepidopteran, leg fragments of orthopteran, tipulid larva, centipede, spider. Dip-terous and lepidopterous remains form the major portion (in one case 60 per cent). Animals caught in traps showed preference for meat bait. Nothing known directly of methods of catching food, but there is much anatomical evidence which will be discussed below.

4. *Locomotor habits.* Only definite fact of field observation is that animals move about freely and are terrestrial, often going through runways. Much anatomical evidence.

5. *Protective habits and reactions.* No direct testimony.

6. *Breeding habits.* Ditto.

## II. HABITUS AND HERITAGE OF THE FOOD-GETTING AND FOOD-REDUCING SYSTEMS

### A. *Habitus*

The food habitus involves primarily the organs of detection, prehension, occlusion, mastication, deglutition, ingestion, digestion, assimilation, circulation and excretion. It involves secondarily other systems, such as the locomotor and the controlling or nervous, adjusting systems.

*Cænolestes* feeds on insects by means of the following adaptive characteristics:

#### 1. *Organs of detection.*

a. *Sight* poor. Eyes small, orbits small, optic nerves and foramina and nerves of eye-muscles all small.

b. *Smell* very highly developed. Very large olfactory bulbs and tuberculum olfactorium. Chiefly an olfactory brain. Large olfactory fossa in braincase and large snout. Expanded olfactory chamber with four large ethmoturbinals and one nasoturbinal.

c. *Touch.* Sensory vibrissæ on snout and cheeks. Very large superior maxillary branch of fifth nerve for nose and lips.

d. *Hearing* acute. Very large external ears and large inner ear.

#### 2. *Organs of prehension and occlusion.*

a. *Prehension.* Orbicularis oris and buccinator muscles well developed. Maxillo-labialis or levator muscles of lips rather weak. Labrets on upper and lower lips recall those of kangaroos. May be used for holding or ejecting food? Tongue long, fleshy, pointed, under surface sharply keeled, the keel extending beyond the tip of the tongue, fitting into the interspace between the two long anterior incisors. It represents the median portion of the sub-lingua (Lönnerberg).

b. *Prehension and occlusion.* Upper and lower incisors remarkably kangaroo-like for prehension and cutting. Large papilla incisiva, also kangaroo-like. Opposes lower incisors. Incisor arrangement functionally more or less shrew-like. Palatal ridges closely resembling those of the Macropodidæ and *Eudromicia* among the Phalangeridæ (Lönnerberg). Upper premolars small, pointed; coöperate with small lower incisors and lower premolars to kill insects.

### 3. *Organs of mastication.*

a. Upper and lower molars (Fig. 1. Description by present writer):  $m_1$ - $m_3$  tuberculosectorial, with expanded posterior V and large talonid basin. The large talonid implies a large protocone in the upper molars;

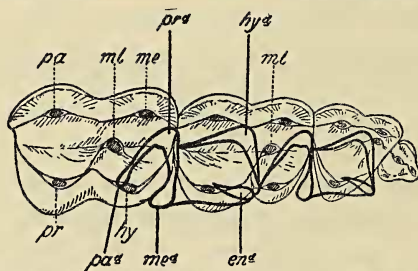


FIG. 1. DIAGRAM SHOWING OCCLUSAL RELATIONS OF THE PARTS OF THE UPPER AND LOWER MOLARS.

The metacone (*me*) and metaconule (*ml*) of the upper molars have their normal spatial relations with the parts of the lower teeth.

UPPER MOLARS		LOWER MOLARS	
<i>pr</i> , protocone	<i>Trigonid</i>	<i>Talonid</i>	
<i>pa</i> , paracone	<i>pr</i> <sup>d</sup> , protoconid	<i>hy</i> <sup>d</sup> , hypoconid	
<i>me</i> , metacone	<i>pa</i> <sup>d</sup> , paraconid	<i>en</i> <sup>d</sup> , entoconid	
<i>ml</i> , metaconule	<i>me</i> <sup>d</sup> , metaconid		
<i>hy</i> , hypocone			

the greater transverse width of the talonid as compared with the trigonid invariably implies that the para- and metacones are well separated. The fact that the trigonid basin is well above the level of the talonid basin implies that the protocone is higher than the hypocone. The marked anteroposterior length of the first three lower molars implies a corresponding lengthening of the upper molars.

There is practically no trigonid basin in the fourth lower molar and so there should be, and indeed there is, no hypocone on the third upper molar. The enlarged entoconid of  $m_{1-3}$  fits lingually between the proto- and the hypocone.

The metaconule (*ml*) of the upper molars furnishes an additional cutting blade that works between the hypoconid of one lower molar and



the protoconid of the one behind it. Doctor Osgood suggests that this small cusp may represent a reduced metacone and that the two main outer cusps are derived from the styles; but, as shown in Fig. 1, the two main outer cusps have practically the normal occlusal relations of para- and metacones, while the stylar cusps of *Perameles* are here represented by the external cingulum. All this arrangement of shearing blades would be well adapted for cutting and dividing the chitinous bodies of insects.

The fourth upper and lower molars are reduced in size precisely because the first three are enlarged and because there was no room for expansion backward without encroachment upon the space filled by the strong jaw muscles.

b. *Jaws.* Jaw movements (as inferred from experiments with skulls and mandibles) remind one somewhat of those of herbivores, perhaps because chitinous bodies may be somewhat like grass stems in cutting properties. As shown in American Museum specimens of *Cænolestes*, the lower molars move from below, upward, forward and inward. In using the tip of the lower central incisor the animal brings the condyle forward to the front part of the smooth glenoid; the dorsal edge of the long lower incisor shears past the compressed second and third upper incisors.

Jaw muscles recall artiodactyls and especially kangaroos; but the most exceptional feature is the large size of the external pterygoid which is two-fifths the size of the internal pterygoid and double-headed, inserting at base of mandibular condyle and on stylomandibular ligament. Possibly associated with forward oblique pressure of lower molars on upper.

Bony jaws: upper jaw (including zygoma) on the whole rather more slender than in primitive insectivores; lower jaw with large areas for masseter and internal pterygoid muscles.

4. *Organs of deglutition and digestion.*

- a. Parotid and submaxillary glands very large.
- b. Throat muscles apparently primitive and normal.
- c. Stomach with strongly differentiated glandular area forming a compound gastric gland, comparable in part to *Phascolarctos*, *Phascolomys*, and *Manis*. Stomach unique.
- d. Large intestine relatively short.
- e. Colon short, with very small cæcum.
- f. Liver relatively large.
- g. Pancreas extensive.



*B. Heritage*

Accepting the views of Huxley, Dollo, Bensley, Osgood and others that the existing Didelphidæ stand near the center of the adaptive radiation of the marsupials (a view endorsed by Matthew, 1913, on palæontological grounds) we find that in its nutritional habitus *Cænolestes* is almost intermediate between the primitive insectivorous polyprotodonts and the more primitive Australian diprotodonts, such as *Distæchurus* of the Phalangeridæ. Thus in the dentition it inherits from the polyprotodonts the primitive dental formula, the tuberculo-sectorial character of the lower molars, the remnants of trituberculy in the upper molars, and of the external cingula in both the upper and the lower molars. On the other hand *Cænolestes* has advanced in the direction of the diprotodonts in acquiring fully developed diprotodonty of the front teeth, and a remarkably kangaroo-like papilla incisiva, while the upper and lower molars approach the pattern of those of the smaller phalangers. But neither in *Cænolestes* nor in any of its known extinct relatives is the dentition as a whole sufficiently close to those of Australian diprotodonts to warrant us in referring them to any given Australian family. In comparison with that of *Perameles*, the dentition of *Cænolestes* differs radically; for the former may best be derived as by Bensley (Pls. 5, 6) from some small polyprotodont, such as *Peratherium*, with inwardly grown para- and metacones and heavily developed buccal styler cusps. In the Peramelidæ the dentition, while remaining polyprotodont in front, has become hyposodont in the cheek teeth, while *Cænolestes* has acquired diprotodonty in the front teeth and incipient lophodonty in the cheek teeth. In brief, as regards its dentition, *Cænolestes* and the whole family of Palæothentidæ may represent an independent group not directly ancestral to any Australian diprotodont, but lying between the Peramelidæ and the Phalangeridæ, as suggested by Osgood.

In respect of the organs used in detecting the food, *Cænolestes* may well represent a secondary specialization in the excessive size of its olfactory, tactile and auditory organs and in the reduction of the sense of sight which is fairly well developed in the smaller Didelphidæ.

With regard to the stomach, which is peculiarly specialized, Osgood remarks (p. 72) that this organ is unique and serves to strengthen the general conclusion that the animal stands by itself quite as independently as any of the highly specialized Australian forms. Osgood also remarks (p. 78) that the short colon combined with the small cæcum in *Cænolestes* is contrary to the usual condition in marsupials and is

most nearly met in certain of the dasyures, and that although the short colon is perhaps primitive, the small cæcum is obviously a secondary condition.

In brief, to judge from its nutritional habitus as a whole, one might infer (as Doctor Osgood does) that *Cænolestes* is a descendant of that part of the primitive polyprotodont group which gave rise both to the Peramelidæ and to the Australian diprotodonts.

### III. HABITUS AND HERITAGE OF THE LOCOMOTOR APPARATUS

#### *A. Habitus*

The locomotor habitus involves primarily the locomotor system of nerves, muscles, connective tissue, ligaments, axial and appendicular skeleton. It is supported of course by the activities of the food habitus and is controlled by the nervous system. It subserves the needs of the protective, nutritional and reproductive systems.

Among other significant facts regarding the skeleton as a whole are the following: the head is decidedly long in proportion to the size of the thorax, as in insectivores, and in contrast with most ungulates, in which the head is comparatively small. The thorax is relatively small, perhaps because the food is highly nutritious, and especially because a small animal needs relatively far less food than a large one. The locomotor skeleton must therefore be adapted to the support and propulsion of a large head and a relatively light thorax. Accordingly we find that the backbone has the cervical vertebræ quite short, with a very large lumen for the spinal cord, that the dorsal and lumbar and more proximal tail vertebræ are large, as are also the chief muscles of the back.

*Limbs and feet.* The most conspicuous and easily interpreted parts of the locomotor habitus are usually the extremities. In *Cænolestes* the pes presents a general development similar to that of *Phascogale* in so far as it has a reduced clawless hallux and is rather narrow, with four sub-equal clawed digits. Such a foot is of the sub-cursorial rather than arboreal type, as indicated also in the skeleton of the foot, the astragalus, for instance, being somewhat intermediate between that of the pedimanous marsupials and that of the highly saltatorial forms (Osgood, p. 95). In this connection Osgood notes (p. 60) that "the muscles of the legs and feet in *Cænolestes* are adapted to a terrestrial, almost cursorial life. The leg muscles have short, thick, fleshy parts and very long tendinous extensions, relatively longer even than in such terrestrial

forms as *Phascogale*, and in this respect are perhaps most similar to those of the saltatorial but otherwise generalized Australian polyprotodont *Antechinomys*, the myology of which has not been thoroughly described. The proportion of tendinous to fleshy parts is about as 60 is to 40 and the outline of the leg thus resembles that of a digitigrade animal. It is markedly different from that of *Didelphis*, in which fleshy extensions reach nearly or quite to the carpus and tarsus. Specialization for terrestrial life has proceeded far beyond that in *Peramys*, whose habits are presumably not greatly different from those of *Cænolestes* but whose musculature is only slightly different from that of *Didelphis*. . . . There is some reduction of the intrinsic muscles of the feet, especially in the adductor sets, and the grasping power is distinctly limited." On the other hand we have the opinion of Lönnberg, expressed as follows: "As already known, *Cænolestes* has arboreal habits. Its feet with their naked, warty soles and the well developed pads must be useful in climbing, but the fore feet undoubtedly exhibit more pronounced adaptations to the arboreal life. The reduction of the claws on the first and fifth finger to nails and the displacement of the latter in direction towards the carpus must be interpreted as such adaptations. Although neither the pollex nor the fifth finger are directly opposable, they are certainly more free in their movements than the corresponding fingers in f. i. *Phascogale* or some other primitive marsupial. They serve therefore without doubt as useful grasping organs, and the fifth finger appears to do so even in a higher degree than the pollex itself, to judge from the fact that it is more powerful and has a better developed pad at its base."

In brief, if *Cænolestes* can climb trees at all it does so not by means of the primary arboreal habitus of the Didelphidæ and Australian diprotodonts, which have well developed divergent hallux and pollux, but by a secondary arboreal adaptation involving sharply curved claws on the middle three digits of both manus and pes, with strong, deep flexors of the digits and partly divergent pollex and minimus in the manus. On the other hand, it is perhaps more probable that the strong claws on the hands and feet may be used in scratching for insects on the ground. Taken as a whole the limbs and feet resemble those of rats and insectivores, especially in such particulars as the bowing of the tibia upon the fibula, and of the radius on the ulna, with the reduction of free movement in both cases.

Important indications concerning the method of locomotion are afforded by the following data supplied by Osgood: In *Cænolestes* the



tibia is very long, the femur being only 63.5 per cent as long as the tibia, i.e., nearly as long as in the saltatorial *Macropus giganteus* in which the femur falls to 57 per cent of the length of the tibia. This contrasts with *Perameles nasuta* in which the femur is 94.3 per cent of the length of the tibia, and still more with *Sarcophilus*, *Trichosurus*, *Phascalomys* and *Phascolarctos*, in which the percentage rises rapidly from 100 to 134.

Other indications of cursorial or partly saltatorial modes of locomotion may be found in the large size of the lumbar vertebræ, which have well-developed, forwardly-directed parapophyses, in the length of the tail and large size of the caudal centra and chevrons, in the fact that the ilium is nearly parallel with the sacral portion of the column as in the kangaroos. There is a distinct so-called center of motion located in an anticlinal vertebra, in the posterior dorsal region, as in *Dasyuridæ*, *Macropodidæ* and other terrestrial or leaping forms, and in contrast with the primitive arboreal *Didelphidæ* in which there is practically no anticlinal vertebra.

In brief, the evidence for cursorial and probably in part saltatorial habits seems fairly conclusive, but it is also barely possible that these small and very active animals run up the trunks and branches of trees.

### *B. Heritage*

That *Cænolestes* has been derived eventually from *Didelphis*-like arboreal forms, in accordance with the views of Dollo and Bensley with regard to marsupials as a whole, is evidenced by the occurrence of many primitive marsupial characters in the locomotor apparatus, such as are found in the *Didelphidæ* in association with arboreal habits. Even the hands and feet retain evidences of ultimate derivation from a *Didelphis*-like prototype. In the pes perhaps the closest resemblances are to be found in *Phascogale*, but although the underlying pattern is similar, a significant difference is seen in the larger size of the volar pads in *Cænolestes*, which is possibly associated with a scratching or scraping action of the feet.

In the postcranial skeleton of *Cænolestes* Osgood (p. 98) notes a number of peculiar or unique characters which perhaps collectively indicate a long separation from other families of marsupials. Even the resemblances to others are distributed in such a way and are accompanied by so many differences that *Cænolestes* cannot easily be made to fit in either with the *Polyprotodontia* or the *Diprotodontia*. On the whole, the postcranial skeleton suggests a nearer relationship with

Australian marsupials of both divisions than with the Didelphidæ. There are also certain special resemblances to the Peramelidæ (Osgood, p. 150) which, taken in connection with other evidence, leads Doctor Osgood to place the *cænolestids* next to that family.

#### IV. HABITUS AND HERITAGE OF THE REPRODUCTIVE SYSTEM

With regard to the male generative organs of *Cænolestes* Doctor Osgood states (p. 65) that the most noteworthy features are the extraordinary size of the prostate and Cowper's glands, the very deeply cleft glans penis and the absence or great reduction of the levator penis muscle. The bifid glans penis occurs in both polyprotodonts and diprotodonts, and affords no definite evidence of relationship, and the other features also are difficult to interpret.

From the comparative standpoint the female reproductive organs, Doctor Osgood concludes, are more significant than those of the male. They are distinctly of a diprotodont rather than a polyprotodont type. This is evidenced by the deep median vaginæ and the long lateral vaginæ, and Doctor Osgood concludes that so far as gross examination indicates, parturition may take place by a short cut through a secondarily developed direct median passage, as in *Perameles* and the Macropodidæ.

The accessory reproductive characters of the female also afford some slight evidence of relationship with Australian forms, since there are four mammæ, as in many Australian genera, in contrast with the much higher number (up to twenty-seven) in the Didelphidæ. But the excessively high birth rate may be one of the features to which the Didelphidæ owe their survival, and it may therefore be a specialization in that family. On the whole, in the characters of the reproductive system *Cænolestes* shows a closer resemblance with Australian than with known Holarctic forms.

In conclusion, although the zoögeographic bearings of these facts have already been carefully considered by Doctor Osgood, it is to be hoped that he and other specially qualified authorities will further develop the true significance of these Australian-like characters in a South American family.

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